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RESEARCH ARTICLE

Estimating the age of domestic fowl (*Gallus gallus domesticus* L. 1758) cockerels through spur development

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Abstract

Determining the age of bird remains after the cessation of growth is challenging due to the absence of techniques such as tooth eruption and wear available for mammals. Without these techniques, it is difficult to reconstruct hunting strategies, husbandry regimes, and wider human–animal relationships. This paper presents a new method, developed from a collection ($n = 71$) of known-age specimens of domestic fowl (*Gallus gallus domesticus* L. 1758), for assessing age based on the fusion and size of the tarsometatarsal spur. Using this method, we reconstruct the demographics of domestic fowl from Iron Age to Early Modern sites in Britain to reveal the changing dynamics of human–domestic fowl relationships. We highlight the advanced age that cockerels often attained in their early history and how their life expectancies have subsequently declined.

KEYWORDS
aging, chicken, sexing, spur development, zooarchaeology

1 | INTRODUCTION

Determining the age of animals represented within archaeological assemblages is essential for understanding hunting strategies, husbandry regimes, and wider human–animal relationships (Ruscillo, 2015; Wilson et al., 1982). However, while the aging of mammals has received much attention (e.g., Grant, 1982; Jones & Sadler, 2012; Moran & O'Connor, 1994; Popkin et al., 2012), methodologies for aging avian remains are less well developed.

Ascertaining a bird's age antemortem is relatively straightforward: Most exhibit age-related variation in size, plumage, vocalizations, and social and sexual behavior (Ottinger, 1983; Owens & Hartley, 1998; Pettingill, 1985). Age estimations from skeletal remains are more challenging. Unlike mammal bones, bird bones have a low number of fusion points after hatching (Hogg, 1980). Bird long bones possess no epiphyseal centers of ossification; instead, the whole epiphysis remains cartilaginous during growth (Silver, 1969).

Recent attempts have been made to refine age estimations of young domestic fowl (*Gallus gallus domesticus* L. 1758) based on morphological and metrical analysis of the developing skeleton (Thomas et al., 2016), yet the absence of aging techniques applicable to mammals—such as dental eruption and wear patterns—renders estimations beyond age classes of "chick," "juvenile," or "adult" difficult.

As with many other avian species (e.g., Nelson & Bookhout, 1980; Broughton et al., 2002), the number of circumferential cell layers (growth rings) present in domestic fowl bones shows no correlation with age (van Neer et al., 2002). Pathologies typically associated with senescence such as enthesophytes and degenerative joint disease may provide an indication of advanced age (Serjeantson & Morris, 2011), but their occurrence may be attributable to nutritional factors, dysplasia or pathogens (Fothergill, 2017; Fothergill et al., 2017; Sokoloff, 1959). There is, therefore, a need for osteological aging methods that allow routine assessment of bird age after the cessation of growth.

The development of osseous spurs on the caudomedial aspect of tarsometatarsi in male Galliformes, such as domestic fowl, offers an opportunity for achieving such a method. The presence of spurs is the primary method of identifying cockerels[1] zooarchaeologically, although there remains uncertainty on the timing of their development and the potential for misidentifying young males (Allison, 1985; Doherty, 2013; Sadler, 1991; Sykes, 2012; West, 1982, 1983). Spurs may also develop in hens, driven by both a genetic predisposition of certain breeds (Boyer, 1917; Christmas & Harms, 1982) and abnormal endocrine function in later life (Domm, 1927; Fairfull & Gowe, 1986; Hutt, 1949; Morgan, 1920). External spur length is commonly

TABLE 1 Tarsometatarsus aging: Comparison of timing data from studies of known-age domestic fowl and cross-bred junglefowl

Breed	*n*	Sex	Method	Timing	Study
Proximal fusion of tarsometatarsus					
Golden Cornet	45	F	X-ray	2.7–3.7 months	Hogg (1982)
Ross broiler	10	M	X-ray	3.2 months	Breugelmans et al. (2007)
White Leghorn	[a]	F	X-ray	3.2–3.4 months	Hogg (1982)
White Leghorn	[a]	M	X-ray	3.7–3.9 months	Hogg (1982)
Rhode Island	[a]	M	X-ray	3.9–4.6 months	Bruce et al. (1946)
New Hampshire × Barred Rock	30	M&F	X-ray	4 months	Church & Johnson (1964)
White Leghorn	[b]	F	Gross	4.5 months	Latimer (1927)
Rhode Island × Light Sussex[c]	101	M&F	Gross	4.5 months	Wilson (1954)
Rhode Island	1	F	X-ray	5 months	Breugelmans et al. (2007)
Cross-bred Red Junglefowl	17	F	Gross	5 months	Thomas et al. (2016)
Cross-bred Red Junglefowl	25	M	Gross	5.9 months	Thomas et al. (2016)
White Leghorn	[b]	M	Gross	6.5 months	Latimer (1927)
Beginning of ossification of the spur core					
New Hampshire	5	M	X-ray	7 months	Juhn (1952)
New Hampshire × White Plymouth Rock	15	M	X-ray	7 months	Juhn (1952)
Barred Rock	3	M	X-ray	8 months	Juhn (1952)
Development of bone on tarsometatarsus shaft					
Old English Game × Light Sussex	2	M	Gross	6 months	Doherty (2013)
Maran	1	M	Gross	Absent at 8 months	Sykes (2012)
Cross-bred Red Junglefowl	1	M	Gross	8 months	Thomas et al. (2016)
Not specified	[a]	M	X-ray	9 months	Juhn (1952)
Light Sussex	4	M	Gross	Absent at 13 months	Doherty (2013)
Light Sussex	1	M	Gross	Absent at 15 months	Doherty (2013)
New Hampshire[d]	3	M	X-ray	18 months	Juhn (1952)
White Plymouth Rock × Barred Rock[d]	1	M	X-ray	30 months	Juhn (1952)
Fusion of spur core to shaft					
Old English Game × Light Sussex	4	M	Gross	9 months	Doherty (2013)
New Hampshire	5	M	X-ray	Unfused at 12 months	Quigley & Juhn (1951)
Dorking	1	M	Gross	Unfused at 34 months	Sadler (1991)
Red Dorking	1	M	Gross	Unfused at 85 months	Sadler (1991)

[a]No data.
[b]Latimer (1927) analyzed 97 skeletons although the number of each sex is not presented.
[c]Wilson (1954) did not directly examine the fusion state but observed no change in bone length after 4.5 months.
[d]Juhn (1952) indicates a "socket" is present, though as Sadler (1991) notes, this could either mean the spur is not fused to the shaft or fused and surrounded by bone.

employed to estimate the age of live pheasants, partridges, and turkeys (Badyaev et al., 1998; Gates, 1966; Koubek & Hrabe, 1984; Pépin, 1985; Stokes, 1957; Woodburn et al., 2009). While in these Galliformes spur length is closely correlated with age (Lucas & Stettenheim, 1972), Louvier (1937) observed that in domestic fowl, the use of an arbitrary spur length as an indicator of a certain age would ignore other factors that could impact length, particularly the diverse size of breeds. Instead, spur length must be examined in relation to the greatest length of the tarsometatarsal.

In an attempt to further our understanding of how human–chicken relationships changed through time, this paper reviews the timing of spur development and growth through the analysis of tarsometatarsi from known-age and sex individuals from modern (i.e., non-archaeological) specimens and sets out a method for estimating age based upon the relationship between spur and tarsometatarsal length.

2 | DEVELOPMENT OF THE TARSOMETATARSAL AND SPUR IN DOMESTIC FOWL

The constituent elements of the tarsometatarsal (distal tarsals and metatarsals I–V) unite *in ovo* and ossify during prenatal and early postnatal life. The bone expands rapidly after hatching, doubling in length within the first month (Church & Johnson, 1964; Latimer, 1927; Wilson, 1954). Cessation of longitudinal growth and disappearance of the proximal growth plate occur between 3 and 6 months, depending on breed (Table 1) but continue to increase in diameter for 1–2 months after attaining its maximum length (Wilson, 1954).

In mammals, the timing of epiphyseal fusion may be delayed by castration, which elongates the growing period resulting in longer and broader bones in the appendicular skeleton, particularly those where epiphyseal closure occurs late, such as the tarsi (Davis, 2000; Hammond & Appleton, 1932; Hatting, 1983; Moran & O'Connor, 1994; Noddle, 1974; Popkin et al., 2012). Although it has long been asserted that the same occurs with the castration of cockerels, termed caponization in fowl (West, 1982), this is unsupported by the evidence. Only Hutt's (1929) observations of 105 cockerels and 16 capons report that the greatest length of bones in capons are larger than those of cocks (tarsometatarsal on average 3.9 mm longer), in contrast to all other studies (Chen et al., 2006; Landauer, 1937; Mausi & Hashimoto, 1927; Pirsche, 1902; Sellheim, 1899). As Landauer (1937) notes, Hutt's results were likely influenced by the method of sample collection: the groups are highly unbalanced; it is not clear whether all the birds were of comparative age; and included both "below standard weight" Brown Leghorns and "larger on average" White Leghorns from separate flocks with no indication of how they are distributed between each group (Hutt, 1929, p. 203). Disregarding this study, as Hutt (1949, p. 253) later appears to, it can be concluded that mature capons and mature cockerels attain the same skeletal dimensions. There is, however, limited evidence that true caponization, achieved by removal of the testes rather than simply cauterizing the spur, was practiced until the early modern period and likely carried a high risk of mortality (Cvjetkovic et al., 2017; Peters, 1997, 1998).

In contrast to all other skeletal elements which do not undergo gross remodeling during life, the tarsometatarsal of the cockerel is unique by developing an osseous spur on the caudomedial aspect after attaining skeletal maturity. Development of the spur proceeds as follows (Figure 1):

1. Morphogenesis begins *in ovo*, with cockerels developing modified epidermal scutes in which the bony spur later forms (Louvier, 1937; Puchkov, 1979; Smoak & Sawyer, 1983). Almost all healthy cockerels develop spurs apart from those with a rare scaleless (Abbott & Asmundson, 1957) or spurless mutation (Kozelka, 1933), which both markedly shorten life expectancy. Some types may develop multiple spurs, notably the Sumatran Gamefowl, which may have as many as five, each with their own sheath (Hutt, 1941; Washburn & Smyth, 1971). At hatching, the outer sheath measures approximately 0.5 mm in length, gradually increasing to 20–30 mm by 12 months in modern commercial breeds (Juhn, 1952; Louvier, 1937; Quigley & Juhn, 1951) (Figure 1a).
2. At a certain point, ossification of the spur core begins (Figure 1b). Calcified granules form 4–6 mm from the shaft, organizing into a diminutive central core (Juhn, 1952). Ossification begins at the proximal tip, growing distally towards the shaft (Evans, 1952; Juhn, 1952).
3. After reaching a critical distance from the shaft, the core projects bony swellings that reach out and fuse with the shaft (Juhn, 1952; West, 1983). In response, the previously smooth tarsometatarsus develops extra bone—a spur scar—that meets and fuses to the advancing core (Figure 1c). The development of extra bone on the tarsometatarsus appears to be stimulated by the core, as its removal prior to contact will prevent the bony formation (Evans, 1952; Hutt, 1949). Similarly, if transplanted elsewhere and in contact with bone, the core and sheath continue to grow but remain unattached to the skeleton (Kozelka, 1933). During fusion, it is common for only a portion of the core to fuse to the shaft and the remainder curves around the tendons, which extend down the posterior surface of the bone, forming a "spur shield" (Sadler, 1991).
4. The fused spur continues to increase in length and diameter after fusion, although the growth lags behind that of the keratin sheath, with the bone occupying an ever-smaller portion (Juhn, 1952). As it grows, the sheath often curves towards the dorsal region of the body (Figure 1d).

The timing of this process is highly variable, with considerable inter- and intrabreed variability. However, the overarching observation is that ossification of the spur core and its subsequent fusion to the shaft occurs long after the bird has reached sexual maturity and after complete ossification of the tarsometatarsus (Juhn, 1952). Radiographic analysis of known-age individuals by Juhn (1952)

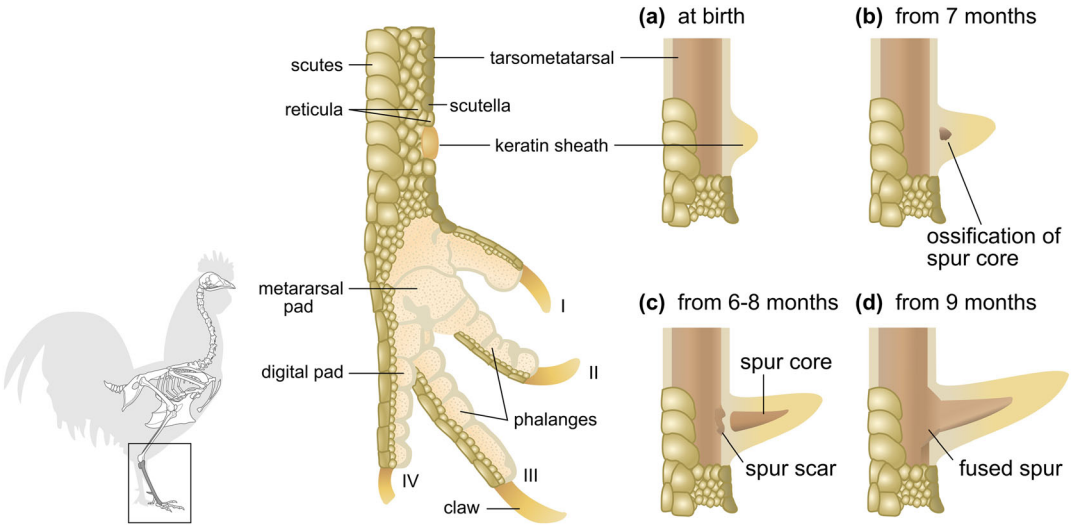

FIGURE 1 Development of the tarsometatarsal spur in male domestic fowl: (a) the keratin sheath in which the bony spur later forms is present at hatching; (b) ossification of spur core begins with calcified granules organizing into a central core, beginning at the tip, and growing towards the shaft; (c) at a certain distance, the previously smooth tarsometatarsal projects bony swellings (a spur scar), which meets and fuses to the advancing core; (d) the fused spur increases in length and diameter after fusion, with the keratin sheath often curving towards the dorsal region of the body [Colour figure can be viewed at wileyonlinelibrary.com]

indicated that ossification of the core did not begin until 7–8 months of age, with bony projections from the shaft commencing at 9 months. Osteological analysis by Doherty (2013) identified a spur scar in a 6-month-old cockerel but recorded total absence in individuals aged 13 and 15 months. Complete fusion of the core to the shaft has been seen as early as 9 months (Doherty, 2013) and not finalized by as late as 85 months (Sadler, 1991) (Table 1).

The rate of growth after fusion is similarly unclear. Louvier (1937) suggested, and later repeated by Habermehl (1975), that by 12 months of age, the external length of the spur (i.e., including the spur sheath) should be approximately 15 mm in length, growing 10–15 mm annually. This is in line with Washburn and Smyth's (1971) suggestion that a 3- to 4-year-old cockerel would have a keratinous spur of 50 mm. However, Louvier (1937) acknowledged that external spur length alone is a poor indicator of age as it fails to recognize inter- and intrabreed variability in tarsometatarsus length: at 12 months of age, external spur length from 11 to 18 mm in Leghorns, 11 to 19 mm in Bresse Noire, and 12 to 16 mm in Orpingtons.

The development of the spur is heavily influenced by the endocrine secretions of the gonads and thyroid. Although the overall size of the tarsometatarsus is unaffected by caponisation, full or partial removal of the testes may result in the formation of longer and sharper spurs (Domm, 1927; Finlay, 1925; Quigley & Juhn, 1951) although others contend that the keratinous and osseous spurs of the capon are indistinguishable from those of the cockerel (Beuoy, 1921; Goodale, 1916; Yarrell, 1856). The most authoritative work comes from the radiographic imaging of a single flock of identical age by Quigley and Juhn (1951) who observed the unfused spur core to be on average 3 mm longer in capons than cockerels at 12 months of age.

The reasons for this are unclear, as the diminution of testosterone retards the growth of other sexual ornamentation such as the comb and wattle. Unconvincingly, Finlay (1925) suggests that longer and sharper spurs may be in part due to the docile nature of capons, with the spur in normal males being worn blunt by fighting and scratching. West (1982) suggests that it may be due to the extended growing period resulting from delayed epiphyseal fusion, although again unlikely considering calcification of the core does not begin until the cessation of tarsometatarsus growth. A possible explanation is that caponization disrupts the hormonal regulation of spur growth, which is simultaneously inhibited by the gonads but promoted by the thyroid. Analogous to the removal of the testes accelerating spur growth in cockerels, Domm (1927) observed that removal of the ovaries in previously spurless hens always resulted in the development of spurs, highlighting the constraining effect of gonadal secretions on spur development. When gonad secretions are unchecked due to thyroidectomy or administration of a thyroid hormone antagonist, both sexes develop smaller, blunter spurs, which remain unfused to the tarsometatarsus (Blivaiss, 1947; Caridroit & Regnier, 1944; Juhn, 1946, 1952).

3 | MATERIAL AND METHODS

Analysis was undertaken on 71 modern tarsometatarsi from domestic fowl and red junglefowl of known-age and sex from multiple U.K. and Ethiopian collections (Table 2). Where available, accompanying biological and husbandry data (breed, color, weight, and pathologies) were recorded for each specimen. Domestic fowl of a wide variety of types were included to enable the method application to a wide geographic

TABLE 2 Demographic composition and sample size of domestic fowl collections considered in this study

		Age group (months)										
Collection	**Sex**	**<6**	**7–9**	**10–12**	**13–24**	**25–36**	**37–48**	**49–60**	**61–72**	**73–84**	**>100**	**Total**
AF	M		1						1		1	3
	F				1	1						2
	Total		1		1	1			1		1	5
ARCCH	M					2						2
	Total					2						2
HE	M	1	3	1	2	1						8
	F		1			1	3					5
	Total	1	4	1	2	2	3					13
JM	M		2									2
	Total		2									2
LBL	M	2	2	2	6	1	2	2				17
	F			2	4	3		1	1	1	1	13
	Total	2	2	4	10	4	2	3	1	1	1	30
NHM	M		2									2
	F		1									1
	Total		3									3
PS	M					1				1		2
	Total					1				1		2
SD	M	2	1	1	4							8
	Total	2	1	1	4							8
SHD	M			1		1			1	1		4
	F				2							2
	Total			1	2	1			1	1		6
Grand Total		**5**	**13**	**7**	**19**	**11**	**5**	**3**	**3**	**3**	**2**	**71**

Abbreviations: AF, Alison Foster's personal collection; ARCCH, Authority for Research and Conservation of Cultural Heritage, Ethiopia; HE, historic England zooarchaeology reference collection; JM, James Morris' personal collection; LBL, University of Leicester Bone Laboratory; NHM, Natural History Museum bird collection, Tring; PS, Peta Sadler's personal collection; SD, Sean Paul Doherty's personal collection; SHD, Sheila Hamilton-Dyer ARCHZOO reference collection.

area. Left-sided tarsometatarsi were preferentially selected, although if not available or was pathological, the right side was analyzed.

Dimensions of the tarsometatarsus—greatest length (GL), breadth proximal (Bp), breadth distal (Bd), smallest diameter of the corpus (SC) and spur length (SP)—were recorded following the protocol outlined in Cohen and Serjeantson (1996). Measurement of the spur was taken up to the tarsometatarsus shaft but did not include the shield, which may form towards the anterior aspect of the shaft (Figure 2). Full biological, husbandry, and metrical data are provided in Table S1.

In order to reconstruct archaeological age and sex profiles, measurements were compiled from 1366 domestic fowl tarsometatarsi from British sites dating from the Iron Age to modern period (specimen information and metrics provided in Table S2). Of these, 346 (25.3%) had spurs, 96 (7%) had a spur scar, and nine (0.7%) had documented medullary bone—a secondary bone that accumulates in the medullary cavity of skeletal elements of female birds as a calcium store for the production of egg shell during the laying season (Driver, 1982). The sex of the remaining 915 (67%) unspurred tarsometatari was inferred through metrical comparison with those exhibiting sex-specific traits (Figures S1 and S2). The strong sexual dimorphism in red junglefowl (*G. gallus*) has been maintained in their domesticated progeny—although less pronounced (Remeš & Székely, 2010)—and manifests as longer and broader bones in the cockerel, with the weight-bearing tibiotarsus and tarsometatarsus showing the greatest difference in size (Hutt, 1929; Merritt, 1966). As noted earlier, spurs can develop in hens, and nine of the spurred tarsometatarsi examined are of a diminutive size to suggest they were female or bantams. Biometric bimodality may not always denote sexual dimorphism and may indicate the presence of birds deriving from morphologically distinct populations (de Cupere et al., 2005). Therefore, sex estimations were made within discrete time periods on a site-by-site basis. SP is not routinely recorded or published, and only 160 specimens had both GL and SP measurements.

4 | RESULTS AND DISCUSSION

4.1 | Timing of spur fusion

Table 3 presents the fusion state of known-age cockerels from this study synthesized with those from published analyses. Of the seven cockerels aged ≤6 months old, only one (14.3%) had developed a spur scar, supporting the indication that formation of the spur occurs after ossification of the proximal epiphysis (Juhn, 1952). One (2.7%) of the 37 cockerels aged between 7 and 9 months exhibited a spur scar, whereas five (13.5%) had fully fused spurs.

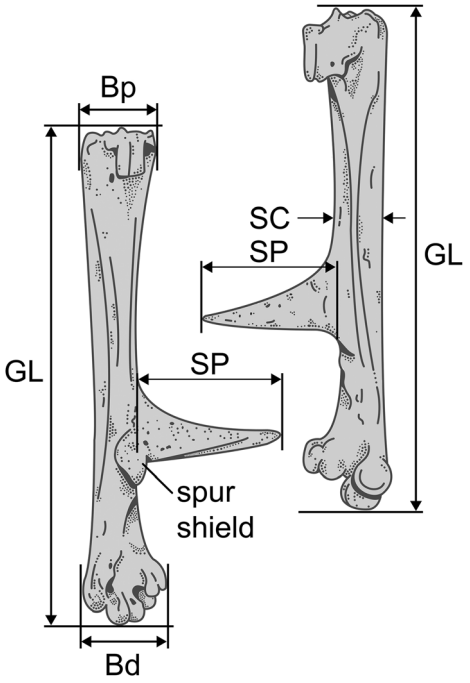

FIGURE 2 Location of measurements taken on the tarsometatarsus as outlined in Cohen & Serjeantson (1996). GL, greatest length; Bp, breadth proximal Bd, breadth distal; SC, smallest diameter of the corpus; SP, spur length

Of the seven that developed a scar or spur within the first 9 months, five were pure or crossbred Old English Game birds, a breed synonymous with cockfighting. Old English Gamecocks have long been highly prized by cockers for their "natural and irresistible passion for fighting" (Jull, 1927) and physique of a small stout body with long legs (Oxford Old English Game Fowl Club, 1920); important qualities for a successful fighting cock where agility and size are essential. With the cockfighting pedigree of the Old English Game, it is tempting to suggest that it may have also been selected for early spur formation.

Seven (28%) cockerels aged 10–12 months, and three (33.3%) of those aged 13–15 months had developed a spur. The presence of spurs increases considerably around 2 years of age, with 11 (84.6%) males aged 18–24 months exhibiting spurs, although two (15.4%) had still not developed a scar. All six cockerels aged between 26 and 34 months were spurred, although the tarsometatarsus of a 34-month-old Red Dorking (PS 02) still only presented a spur scar. Of the five cockerels aged 48–60 months, three (60%) were spurred, whereas a Dorking continued to exhibit only a scar, and a 60-month-old Japanese Bantam (LBL 652) had developed a spur core but remained unfused to the shaft and had left no discernible scar. The latter bird was raised by an experienced breeder and in peak physical condition prior to death (S. Elliot pers. comm.), and it is therefore likely that genetic factors are responsible for the lack of spur development in this individual. The only age group in which all cockerels presented fused spurs was those aged ≥72 months.

These results confirm the late occurrence of tarsometatarsal spurs and the challenge of identifying cockerels morphologically, with the potential that some archaeological specimens could be mis-identified as female while exhibiting very male behavior in life (Sykes, 2012).

TABLE 3 Percentage of tarsometatarsals with either a scar or spur in male domestic fowl of known-age

Tarsometatarsi								
				Spurred				
	Total	Unspurred		Scar		Spur		Combined
Age (months)	*n*	*n*	%	*n*	%	*n*	%	%
5–6 (a)	7	6	85.7	1	14.3			14.3
7–9 (b,c)	37	31	83.8	1	2.7	5	13.5	16.2
10–12 (d)	25	18	72.0			7	28.0	28.0
13–15	9	6	66.6			3	33.3	33.3
18–24 (c)	13	2	15.4			11	84.6	84.6
26–34 (a,c)	6			1	16.7	5	83.3	100
48–60 (a)	5	1	20.0	1	20.0	3	60.0	80.0
72–120	4					4	100	100

Note: Includes data from (a) Sadler (1991), (b) Thomas et al. (2016), (c) Juhn (1952), and (d) Quigley and Juhn (1951).

4.2 | Relationship between spur and tarsometatarsus length with age

Though SP alone is a poor indicator of age, due to inter- and intrabreed variability in tarsometatarsal size (Louvier, 1937), it is possible to compensate for phenotypic variation with the following calculation (Equation 1):

$$\frac{\text{Spur length (SP)}}{\text{Greatest length of tarsometatarsal (GL)}} \times 100. \quad (1)$$

The relationship between (SP/GL) × 100 and age in modern domestic fowl is shown in Figure 3, which presents the data for each individual tarsometatarsus plotted against the specimen's age, with log regression displayed. A statistically significant positive asymptotic correlation is seen between (SP/GL) × 100 and age, with the relative size of the spur increasing with age (Pearson's correlation coefficient = 0.68, P = <0.01). The relative size of the spur increases rapidly over the first 12–18 months after fusion, whereas the subsequent rate of growth is more restricted. Few tarsometatarsi exceeded a (SP/GL) × 100 value of 30, with some individuals aged 24 months showing comparable values with those aged 108–120 months. This suggests that whereas the keratin sheath may grow indefinitely, growth of the bone spur is substantially reduced after reaching approximately 30% of the length of the tarsometatarsal.

Despite the diminutive size of bantam varieties, the relative size of the spur appears to increase analogously to standard types, indicating the applicability of this method to domestic fowl of all sizes. It is also applicable to all sexes. Occasionally, female birds develop spurs, and our study suggests that when present, not only do they attain the same morphology as those of the cockerel but that they also grow at a comparable rate.

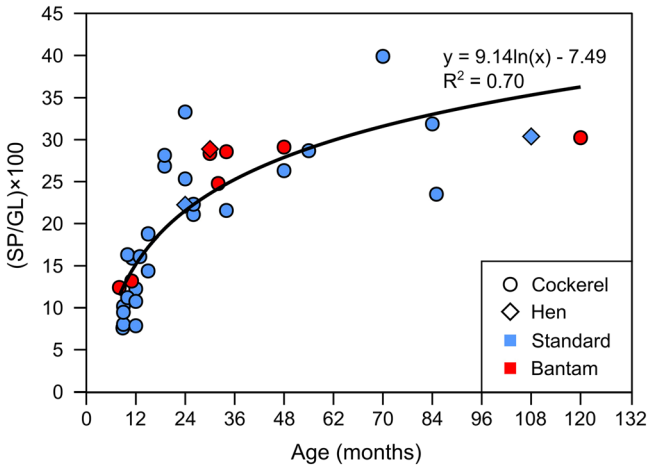

FIGURE 3 Relationship between (SP/GL) × 100 and age in cockerels and hens [Colour figure can be viewed at wileyonlinelibrary.com]

4.3 | Archaeological application

The same formula for relativizing spur length against bone length as a proxy for age was applied to archaeological domestic fowl tarsometatarsi (n = 160). As can be seen in Figure 4, the average age of cockerels increased from the Iron Age/Romano-British transition (4th century BC–AD mid-1st century) to the Early Saxon period (AD 5th–7th century), before gradually decreasing through to the Early modern period (AD 15th–18th century). No spur lengths are reported from modern (AD 18th–20th century) assemblages.

4.4 | Discussion of archaeological data

From their introduction in the Iron Age, the contexts in which domestic fowl remains are recovered suggest that this rare exotica held a special status, one that likely rendered them sacred and above consumption (Sykes, 2012). Few specimens display evidence of butchery, and they are more frequently recovered from individual burials than disarticulated, mixed with other food waste (Morris, 2011). To some extent, this is supported by Caesar's enigmatic observation that Britons kept fowl not for food but '*animi voluptatis*' (1989, p. v.12), a statement widely translated as for spiritual and secular pleasures. The greater importance of their social value (such as deity association, cockfighting, or display of status) over their edibility is underlined by our analysis, which indicates that during the Iron Age/Romano-British transition period, cockerels survived well past sexual maturity. The majority of spurred tarsometatarsi produced (SP/GL) × 100 values comparable with modern birds over 1 year old and many with those that survived into their second or third year. Domestic fowl account for only 0.1% of identified specimens during this period (Figure 5), and it is likely that many of these cockerels were highly prized, such as the articulated skeleton from Houghton Down (Hants.)—recently, radiocarbon dated to the 4th–3rd century BC (Best et al., in press)—which has a (SP/GL) × 100 of 24.1, comparable with birds that survived to at least 2 years of age. Although domestic fowl were more prevalent in the Roman period (AD mid-1st–5th century), they were still a rare commodity, accounting for around 2.6% of identified specimens. Our analysis suggests that the average age of cockerels increased, with the vast majority likely surviving beyond 1 year, and many producing values in line with modern birds aged 2, 3, or 4 years old.

On the basis of combined morphological and metrical sex estimation, we calculate that cockerels account for 67% of tarsometatarsi from the Iron Age/Romano-British transition and 65% from the Roman period (Figure 5). Benecke (1993) observed similar proportions in Early Iron Age assemblages across central Europe where the ratio of cockerels to hens was 3:1 on some of the earlier sites. Benecke (1993) argued that the primary motivation for the introduction and spread of the chicken to central Europe was therefore for meat but probably not for eggs. An overabundance of spurred tarsometatarsi has been noted at several Romano-British sites (e.g., Fothergill et al., 2017; Grimm, 2008; Maltby, 1993;

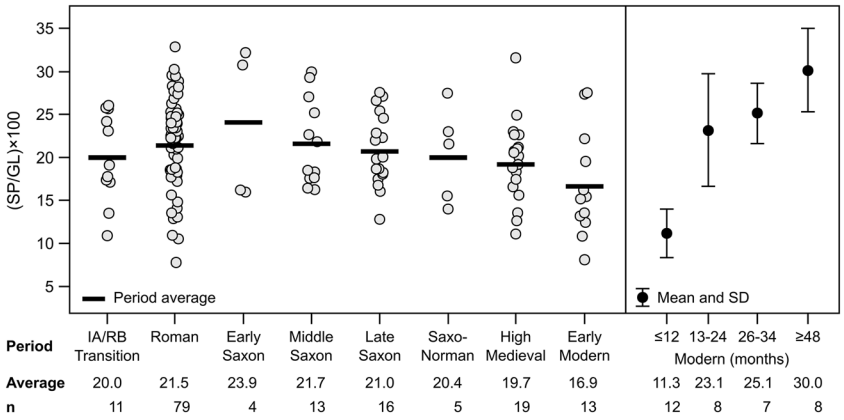

FIGURE 4 (SP/GL) × 100 values across British sites from the Iron Age to Early Modern period and birds of known-age. Iron Age/Romano-British (IA/RB) transition, *4th century BC–AD mid-1st century*; Roman, *mid-1st–5th century*; Early Saxon, *5th–7th century*; Middle Saxon, *7th–9th century*; Late Saxon, *9th–11th century*; Saxo-Norman, *11th–12th century*; High Medieval, *12th–15th century*; Early Modern, *16th–18th century*

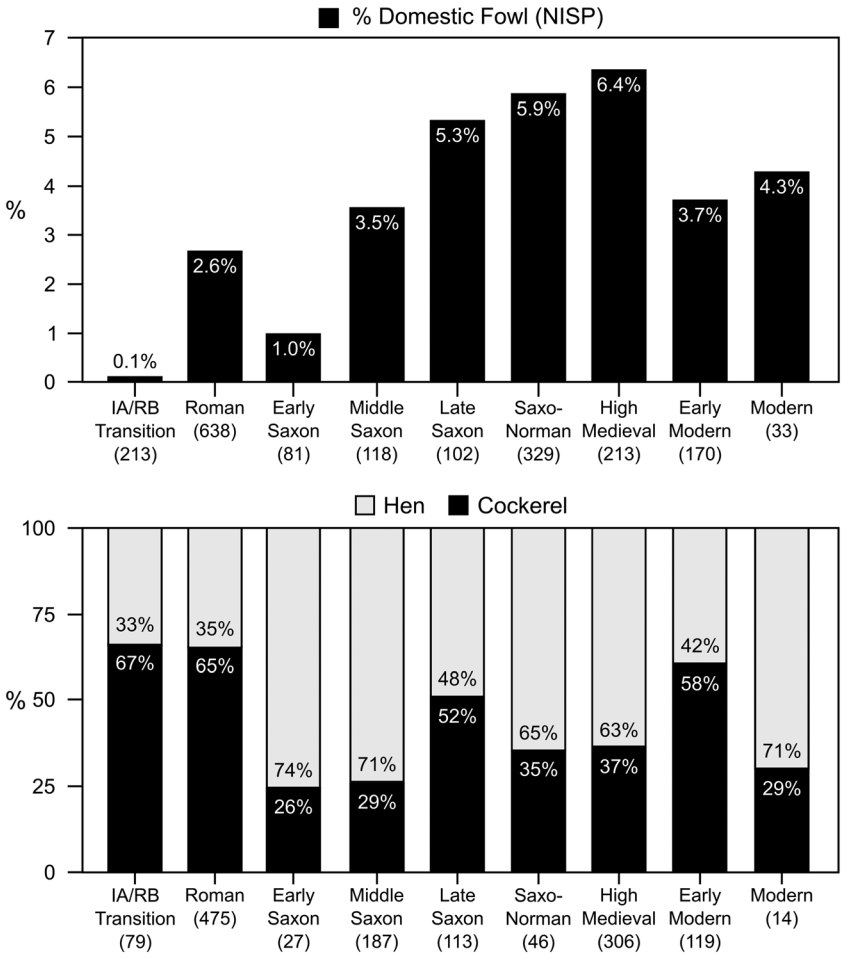

FIGURE 5 (top) Representation of domestic fowl bones from the Iron Age to Modern period based on number of identified specimens (NISP) (Skelton, 2019, number of sites in parentheses) and (bottom) sex ratio of tarsometatarsi based on sexual dimorphism (summarized in Table S3)

O'Connor, 1988; Serjeantson, 2000) and typically interpreted through an economic lens, as evidence for the culling of surplus young males for meat.

However, the data synthesized in this paper indicate that tarsometatarsal spurs develop long after cockerels reach their adult carcass weight. Therefore, cockerels slaughtered primarily for meat (c. 4–6 months) would show no hint of a spur or even a scar. Our analysis of spur length reinforces the idea they lived to advanced ages. With such an abundance of mature cockerels, it may be concluded that most Iron Age and Roman cockerels were kept for reasons other than meat and stock replacement. As Serjeantson (2000) suggested, ritual sacrifice or cockfighting would be good candidates to explain the sex and age profiles. The possibility that cockfighting was practiced by the Romans is supported not only by the zooarchaeological evidence but also by finds of artificial cockspurs from several Roman settlements (Serjeantson, 2000, p. 239; Scott, 1957, p. 157) and provisioning of a cockpit at the Legionary Fortress at Exeter (Bidwell, 1979, pp. 42–43). The abundance of spurred tarsometatarsi in several

temple assemblages, particularly those venerating Mercury and his companion animal, the cockerel (King, 2005), speaks of their religious significance.

The sex ratios of domestic fowl change markedly in the Saxon period. Cockerels account for only 26% of tarsometatarsi from the Early Saxon period (AD 5th–7th century), 29% in the Middle Saxon period (AD 7th–9th century), rising to 52% in the Late Saxon period (AD 9th–11th century), before falling to 35% in the Saxo-Norman period (AD 11th–12th century). The increasing proportion of hens has been noted in multiple archaeological assemblages and is thought to reflect the intensification of meat and egg production (Holmes, 2014; Serjeantson, 2006; Sykes, 2007). This has been linked to Christian fasting practices, which forbade the consumption of meat from four-legged animals but permitted the consumption of birds and eggs (Venard, 2011). Originating in the Benedictine Monastic Order (c. AD 540s), these observances were ultimately adopted by all segments of society by the 10th century as the Church's influence grew (Sykes, 2007) and likely exerted a key pressure on the genetic selection for reduced intraflock aggression and faster onset of egg laying occurring at this time (Loog et al., 2017).

Spur lengths are only available from four Early Saxon tarsometatarsi; two from the secular settlements of Sherbourne House (Gloucestershire) and Stratton (Bedfordshire) are comparable with modern birds aged at least 4 years old, and two from the monastic site of Lyminge (Kent) likely survived into their second year. As their husbandry intensified, average (SP/GL) × 100 values declined during the Middle, Late Saxon, and Saxo-Norman periods, though the majority of cockerels likely survived beyond 1 year old and some considerably longer. Spurred tarsometatarsi are less common at ecclesiastical sites, which may indicate an absence of cockfighting amongst these communities. Depictions of cockerels are rare in Christian Saxon art (Adams, 2015) as are other male animals associated with violence and fertility, such as the stag and boar (Hawkes, 1997). The absence of these motifs along with the faunal evidence suggests a conscious rejection of this activity both symbolically and practically. Lower incidences of mature males may also reflect culinary practices. Immature bones represent choice meat—tender pullets and young cockerels—available to the high-born inhabitants and their guests. Feasting was as important in Saxon monastic life as in contemporary aristocratic culture (Foot, 2006), particularly in those with Royal associations such as Lyminge where juvenile bones account for 18–20% of the domestic fowl assemblage (Knapp, 2019) or Eynsham Abbey where they account for 30–40% (Mulville, 2003).

The decline in the age of domestic fowl in the High Medieval (AD 12th–15th century) and Early Modern period (AD 16th–18th century) is well documented zooarchaeologically, with an increasing proportion of juvenile bones observed at numerous sites (Albarella et al., 2009; Albarella & Murray, 2005; Higbee, 2003; Maltby, 1982; Thomas, 2005). This decline is also seen in (SP/GL) × 100 values, though a few individuals display values comparable only with the oldest modern birds. Cockerels account for 37% of tarsometatarsi in the High Medieval period and 58% in the Early Modern period. An increasing proportion of cockerels in later material has been noted in a number of assemblages (Thomas, 2005; Thomas et al., 2013). Such changes in the sexual composition and age structure of the population of domestic fowl are consistent with a shift in the husbandry strategy, with growing emphasis on meat rather than egg production (Albarella, 1997; Grant, 1988). However, the high proportion of cockerels may also reflect the widespread popularity of cockfighting prior to the 19th century (Griffin, 2005), with cockpits present in most towns and the Royal court (Tolson, 2005).

5 | CONCLUSION

The absence of a routine method for estimating the age of cockerels had previously hindered the study of the dynamics of human–domestic fowl relationships and hidden the great age that many cockerels attained. Given that cockerels are sexually mature by around 4 months of age, the maintenance of large numbers of old cockerels cannot be interpreted in purely economic terms but rather reveals cultural mores and preferences. By developing an aging method based on known-age individuals, there is now the possibility of generating large compatible datasets, and we hope this paper provides the methodological foundations upon which future studies can be built.

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AUTHOR CONTRIBUTIONS

S.P.D., A.F., and N.S. conceptualized the study and conducted the formal analysis. S.P.D., A.F., J.B., S.H-D., J.M., P.S., H.W., R.T., and N.S. provided samples. S.P.D. wrote, reviewed, and edited the original draft and visualized the data. A.F., C.S., R.S., R.T., and N.S. commented upon and edited drafts of the paper.

CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

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ENDNOTE

[1] For simplicity, male domestic fowl of all ages is termed cockerels in this paper. Typically in fowl and cocking nomenclature, a cockerel or stag is a male <1 year old, whereas a cock is >1 year. The informal term rooster may be applied to a male chicken of any age.

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